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Local dispersal of golden-ringed dragonfly

Cordulegaster boltonii

Lokální disperse páskovce *Cordulegaster boltonii*

Diploma thesis

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Prohlášení

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ABSTRAKT

Provedli jsme pilotní studii lokální disperse páskovce kroužkovaného *Cordulegaster boltonii* (Odonata: Cordulegasteridae). Čeleď Cordulegasteridae se vyznačuje mnoha primitivními znaky a spíše omezenou distribuci (minimálně evropské druhy). Zdá se, že navzdory svým fyzickým rozměrům, které je predisponují k vysoké míře pohyblivosti napříč velkým prostorovým měřítkem, je jejich migrace limitována. Linearita jejich habitatu (tekoucí vody lesních potoků), společně s behaviorální ekologii (zvláštní předkopulační chování – skenování potoků, nízkým vytrvalým letem, za účelem vyhledávání samice), vytvářejí unikátní životní strategii, která si zaslouží naši pozornost a přináší mnoho nezodpovězených otázek. Během dvou sezón (2010 a 2011) jsem sbírali data, metodou mark-capture-recapture, v rámci třech oddělených povodí (Dračice, Struha a Koštěnický potok) na lokalitě Přírodního parku Česká Kanada, v jižních Čechách. Patrolující samci *C. boltonii* byli simultánně odchytáváni na všech třech potocích, v celkové délce 9,9 km. Chytili jsme a označili 440 jedinců a zaznamenali 113 zpětných odchytů (26 % "recapture rate") v roce 2010 a 355 bylo označeno a 171 zpětných odchytů zaznamenáno (48 % "recapture rate") v roce 2011. Naše data ukazují na vysokou míru věrnosti samců pro jednotlivé potoky, neboť jsme zaznamenali pouze 10 dlouhých přeletů mezi povodími (2, 8 % míra disperse). Což se též odrazilo na výsledku Craigovy analýzy, která se přiklání spíše k uzavřenosti populace. Patrolující samci se pohybovali v rámci přibližně 250 m „home range". Jednotlivé „home range" se značně překrývají, což vyústilo ve vysokou hustotu samců v rámci některých, evidentně preferovaných, lokalit. Navzdory obecnému očekávání se samci nesnažili ani přemístit z těchto lokalit s vysokou hustotou jedinců, ani se neuchýlili k agresivní obraně teritorii. Lokality méně oblíbené, s menší hustotou výskytu samců byly spíše ponechány opuštěné nebo popřípadě jen vzácně prolétávané (skenované). I přes vzácný výskyty samic na potocích, nebyla pozorována žádná korelace mezi jejich návštěvami a oblíbeností lokalit samci. Stejně tak jsme nenašli žádnou preferenci ve směru letu (po / proti proudu) patrolujících samců. Během sbírání dat jsem pozorovali evidentně nenáhodné chování samců, kdy značná proporce jedinců látala za sebou (ve „vláčcích") v rámci jednominutových intervalů.

Klíčová slova: vážky, Odonata, home range, disperse, mark-release-recapture

ABSTRACT

We carried out a pilot study of local dispersion and patterns of movement of Golden-ringed dragonfly *Cordulegaster boltonii* (Odonata: Cordulegasteridae). *Cordulegasteridae* is a family with many primitive traits present and rather restricted geographical distribution ranges (at least among European species). Their migration seems to be limited despite the body size that predetermines them to high mobility over large spatial scale. Linear habitat (upper parts of narrow forest streams) specialisation along with behavioural ecology (peculiar premating habit of scanning streams for females) is a unique life history, which bring lot of questions. We collected mark-release-recapture data during two adult flight seasons in year 2010 and 2011. We were simultaneously capturing patrolling males along three separate streams (Dračice, Koštěnický and Struha) in total length of 9.9 km in, located in the Natural park Česká Kanada, in the Southern Czech Republic. We captured and marked 440 individuals and recorded 113 recapture events (26 % recapture rate) in year 2010 and 355 individuals were marked, 171 recapture events made (48 % recapture rate) in 2011. Our data suggested high level of stream fidelity (only 10 inter stream dispersal events, 2.8 % dispersal rate). What was as well reflected in a closeness of population estimated by Craig analyse. Patrolling males had home range about 250 m, home ranges had large overlaps that resulted in a high-density male co-occurrence not territoriality. Despite general expectation males rather stayed within favoured and crowded patch than moved into a bit more unfavourable low density patches, which were readily being abandoned. There was not observed a correlation between female (even though very rare) visits and patches favoured by males. We have not found any preference for patrol flight direction (upstream vs. downstream). During sampling we observed interesting behavioural interaction when we found that time schedule of patrolling males on streams in not random and a large proportion of males were patrolling subsequently within one minute interval.

Key words: dragonfly, Odonata, dispersal, mark-release-recapture

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INTRODUCTION

Insects as well as other animals respond to imminent threats and needs through the process of movement. Individuals move to forage, access habitat, to escape unfavourable conditions or to breed (Dunning, 1992; McIvory & Odum, 1988). Movement of individuals from their birth site to their breeding site, as well as the movement from one breeding site to another is referred as dispersal (Ronce, 2007). In general, dispersal can be distinguished into two basic types: density-independent and density-dependent. Density independent dispersal, or as it is often referred to as passive dispersal, take advantage of various forms of kinetic energy occurring naturally in the environment and organisms have usually evolved adaptations for it. It depends on animal vectors, wind, gravity or currents (Nathan, 2001). Density dependent or active dispersal depends on factors such as local population size, competition for resources, habitat quality and size (Johst & Brandl, 1997). As an answer to population density, dispersal may lower the pressure for resources in an ecosystem, and competition for these resources may be a trigger for dispersal (Irwini & Taylor, 2007).

Movement and dispersal play an essential role in an ecology and evolution of species. These two processes drive local, as well as metapopulation dynamics, determine the spatial scale of evolutionary change, and control the organism response to habitat fragmentation and climate change (Dieckmann, O'Hara, & Weisser, 1999; Bullock, Kenward, & Hails, 2002). As landscapes become more fragmented and species numbers continue to decline, the understanding of movement and dispersal processes becomes increasingly important (Baguette, Petit, & Quéva, 2000; Petersen, Masters, Hildrew, & Ormerod, 2004).

1 DISPERSAL BY FLIGHT

Being extraordinary fliers, adult dragonflies can be expected to exhibit outstanding powers of dispersal. But still, very little is known about nature of this

behaviour. Before the driving mechanism of odonates dispersal can be investigated, it is essential to understand differences between basic flight movements performed by Odonata. First let's distinguish between trivial and non-trivial flights.

Trivial flights are relatively brief, short-range movements associated with an obvious, immediate goal, such as thermoregulation, escape, foraging or reproduction (Johnson, 1969).

Non-trivial flights normally play a major role in the maintenance of the life-cycle. In a contrast with trivial flights, they are longer, straighter, and undisturbed by such immediate goals. Four kinds of non-trivial flight have been distinguished. Each plays different ecological function.

1.1 TYPES OF NON-TRIVIAL FLIGHT PERFORMED WITHIN A SINGLE GENERATION: A PROVISIONAL CLASSIFICATION FROM CORBET (1999)

Type 1. Maiden flight

A one-way flight from the emergence site to the first resting site. Can vary in length between 1 and at least 500m. Performed by the teneral (newly emerged, reproductively immature) adults. Occurs once per generation. The flight appears to be oriented away from water. All Odonata exhibit it.

Type 2. Commuting flight

A two-way flight practised daily, weather dependent, between the roosting sites and the foraging and reproductive sites. Each flight has an obvious goal, driven by an adult's physiological state. Its length can vary between a few metres and more than a kilometre.

Type 3. Seasonal-refuge flight

A two way flight between the emergence site and a refuge that offers a suitable environment in which foraging and reproductive maturation can take place. Usually during the hot, dry summer (Samraoui, Bouzid, Boulabahl, & Corbet, 1998). A regular feature of certain Mediterranean species.

Type 4. Migration

A one-way flight between the emergence site and a new reproductive site. It may be obligate or facultative and occurs only once per generation. Migration can cover distances up to several thousand kilometres.

Most of insect dispersal studies have concentrated on Lepidoptera with just a few on Odonata, especially Anisoptera. However, odonates are particularly good study organisms. They are large, easily handled and marked. Live in a significantly patchy environment, bonded to aquatic habitats for larval development and often spent mature adult life at or near their breeding sites (Rouquette & Thompson, 2007). What should be as well taken into account is that odonates are good fliers and are known to move over large spatial extents (700-4000m) (Stettmer, 1996; Purse, 2003). It's been already shown that odonate movements vary with sex and environmental conditions (Utzeri, 1988), age (Angelibert & Giani, 2003), population density (Rouquette & Thompson, 2007), parasite load and wing length (Conrad, 2002) and distance between resources (Conrad, 1999).

Even though (as it's been said earliert) the primary mechanism for dispersal in Odonata is flight, Angelibert & Giani (2003) documented even cases of dispersal in the egg and larval form. But these are thought to be just an insignificant proportion of dispersal events. Although it is possible that passive dispersal in lotic habitat is common.

1.2 HOW IS DISPERSAL CONNECTED TO REPRODUCTIVE BEHAVIOUR

The adult stage of the Odonata life cycle is relatively short, lasting only a few weeks for most individuals. Since each individual therefore has only a short time to pass its genes on to the next generation, most of adult life is spent maximising the chances of meeting and mating. Mature dragonflies have to meet in time and space. Both genders must be capable to recognise a suitable rendezvous site, which is for

most species as well the oviposition site. The rendezvous is also an arena for sexual selection as a result of male-male completion over high quality oviposition sites. The males of most species of Anisoptera and also Zygoptera show site attachment to various extend. They return repeatedly over a period of time to the same site and defeat it regularly over male competitors of same or even a different species. Within the defended territory, the holder has prior access to females (Corbet & Brooks, 2008).

The degree of site attachment is usually related to male density. Species that occur at low male density at the rendezvous (such as Aeschnidae and Cordulegasteridae) typically shows weak site attachment. Whereas high-male-density species (such as Libellulidae, Corduliidae and Calopterygidae), exhibit strong site attachment (Corbet & Brooks, 2008). At a rendezvous site a male spends most of his time in either non-aggressive flight, searching for females or, if the species shows site attachment, defending the area against other males. Searching may be performed as overlooking the area from a perch, making short forays from a perch or patrolling the site. Patrol flight should increase the chances for male to meet a female. Searching behaviour may be determined by a physical feature of the habitat, such as vegetation or shady/sunny spots, or by a male density (Corbet & Brooks, 2008).

As male density increases at the rendezvous site, there is an increase in the intensity of site attachment and localisation (Poethke & Kaiser, 1987). In addition the size of defended territory decreases (Mokrushov, 1982), as does the duration of occupation (Kaiser & Poethke, 1984). The decrease in territory size reflects the increased energy demand caused by more frequent defend of the territory (Moore, 1987). High male density can eventually lead to a breakdown in territorial behaviour as the territory-defending males are overwhelmed, one of the possible consecutive scenarios are males aggregating in swarms, abandoning territoriality and simply chasing females (Pajunen, 1962; Jacobs, 1955).

1.3 WHY C. BOLTONII?

A surprisingly low number of dispersion and density-dependant behavioural studies were done on true dragonflies (order Odonata: suborder Anisoptera). Most of these studies are concentrating on damselflies (Odonata: Zygoptera). Apparent reason is very simple; as it was mentioned earlier, odonates are extraordinary fliers. In their aerial agility and perfection of flight (especially Anisoptera), they do not have concurrence among animal kingdom, except perhaps few raptorial birds (Wootton, 1992). The bigger the species is, the faster and more mobile it is. One of the measureable physical aspects that has predicative value about their flight ability and is comparable among Odonata suborders is the wing load. Comparative study of wing loading in European Odonata (Grabow & Ruppell, 1995) showed it to be largest in large Anisoptera (lowest in Libellulidae), much lower in Zygoptera (especially Calopterigidae). Because they are such accomplished fliers, it is difficult to track them by direct observation. Methodological problems continuous with task of capturing, that is essential for mark-release-recapture studies.

Cordulegasteridae is a family with many primitive traits present and rather restricted distribution ranges. Even though their size predetermines them to high mobility over large spatial scale, their migration seems to be limited. Linear habitat (upper parts of small streams) specialisation along with behavioural ecology (peculiar premating habit of scanning streams for females/male-male aggressive interaction) is not only an interesting life strategy, but fortunately makes them also rather easy (in a contrast with most of Anisoptera) to handle in a context of mark-recapture survey. *Cordulegaster* fly with considerable less agility than aeschnids and are easy to catch even in feeding flight (Kaiser, 1982). *C. boltonii* has been chosen, because it is the most abundant species from this extraordinary group within our geographic range. And their habitat is in general free of other species of Odonata, means that their behaviour is not influenced by interspecific interactions (interspecific aggression, territoriality), otherwise so frequent within odonates.

1.4 STUDIES OF *C. BOLTONII* DONE UP TILL NOW

A preliminary study of mating strategies was done by Kaiser (1982). It was mainly focused on male intraspecific aggressive and territorial behaviour but contents as well description and records of movement of adult individuals within the studied rivulet. Particularly: patrol flights, daily visits and sequence of male visits during the course of the day. Study was based on 40 marked, 44 recaptured individuals, during six days and a single stream in length of 330 m.

One more MRR study focusing on site-fidelity was carried out by Ott (1988). He discussed adult behaviour with larvae biology with respect to some aspects of nature conservation. (Ott, 1988).

Third MRR study done on *C. boltonii* carried out by Schweighofer (2008) was conducted on 386 male adults marked, 192 recaptured, during two subsequent seasons. Main topic was co-occurrence of *Cordulegaster boltonii* and *Cordulegaster heros* on a small stream in Western Austria, that was recorded for a first time. Study revealed slight differences in patrolling activity patterns between the two species, both seasonally and daily, interpreted as a tendency to mutually avoid peaks in patrolling activity. In addition, data on minimal lifespan and site fidelity of patrolling males were recorded.

In Corbet (2004), there is a reference to personal communication of P. S. Corbet with P. L. Miller (1995), where Miller presents unpublished results of his research of *C. boltonii*. Miller claims that, adult male *C. boltonii* behave territorially at high densities and length of water margin patrolled by territorial males is estimated as 7.5 m within 5-10 m range. But no further details of this survey or any other data are included.

Hykel (2013) deals with the larvae habitat characteristics of *Cordulegaster bidentata* at selected localities in the Western Carpathians Mts. in his Bachelor's thesis. He also carried out MRR study of diurnal activity of matured (Hykel, 2013).

2 AIMS

Our aim was a pilot study of local dispersion and patterns of movement of species with unique life-history, in spatially restricted environments (e.g. rivers, creeks). We tried to cover study area large enough to show us degree of population connectivity; are populations on streams separated, can we talk about stream fidelity or is there exchange of individuals between streams? We know well about existence of phenomenon of male patrol flights, but how much actually do they fly within patrolled stream? What are the home ranges? How long distance can males cover while scanning the stream and how far can they fly between streams, over unsuitable habitat in order to find a new habitat? Do they regularly change their patrolling sites or are they stick to one favourable part of a stream? If they change the sites, is this density-driven? Also, do their home ranges overlap or there is a territoriality among males? Beside this, we were also partly interested in some behavioural interactions. Specifically, during the field survey, we felt into impression that time schedule of patrolling males on streams may not be random, and also we would like to check if they had any preference for patrol flight direction (upstream vs. downstream).

3 MATERIALS AND METHODS

3.1 STUDY SPECIES: *CORDULEGASTER BOLTONII* (DONOVAN, 1807)

Cordulegaster boltonii (Golden-ringed Dragonfly) is the most widespread species of Cordulegasterid dragonflies, an Anisoptera family that is in Europe represented only by the genus Corgulegaster (Lohmann, 1992). In Europe, the genus consists of two-species groups, the *boltonii* and the *bidentata* group (Table 1). Each is a complex of similar species, of which the distribution hardly overlaps. *C. boltonii* is easily recognized by the very large size (70-80mm), yellow-and-black-striped body pattern and the large green eyes meeting at a point above the head (as distinct from the Aeschnids that have a similar appearance and venation)(Fig 1). It typically occurs in lotic habitat, usually in permanent small heath land or moorland streams and brooks. Males and females are similar in colour, but the females have a distinctive, long and robust ovipositor, projecting beyond the tip of the abdomen (Pelt, 2006).

Adult males patrol up and down along small streams, flying low (10-30cm above water surface), often slowly and frequently pausing and settling on overhanging vegetation.

Females are present at streams only for copulation and oviposition. They tend to oviposit alone, repeatedly pushing their strong ovipositor deep into the substrate of the stream, while hovering over shallow water in a vertical position (Merrit, Moore, & Eversham, 1996).

The squat larvae is a shallow burrower, usually living partly in stream detritus and gravel, take two to three years to complete development (Ferreras-Romero & Corbet, 1999).

Flight season is on since the end of May to late August, with a peak in July (Pelt, 2006).

3.1.1 FEEDING FLIGHT

In a feeding flight the *C. boltonii* fly to and fro, often loosely orientated along roads, forest edges or bushes. The flight height varies, often around 1 m, but may be

much higher over vegetation. Flight pattern mostly appear to be rather random, sometimes follows a fixed pattern for a little while. Dragonflies were observed in feeding flight in the immediate vicinity of streams as well as several hundred metres away from it (Kaiser, 1982).

3.1.2 PATROL FLIGHT

Mature males spend up to several hours a day flying up and down along streams in a patrol flight. Flight is rather straight, steady and moderately fast and does not feature hovering. The flight height is mostly 13 to 30 cm above water. Sometimes the males fly in a rather jerky manner. They have tendency to fly in one direction for quite a long distance (up to several hundred metres) before turning and flying the same way back. The change of direction is obviously encouraged by landmarks, such as vegetation overhanging the water. This behaviour gives the impression that male patrols a territory, nonetheless, no individual fixed areas could be identified. Even though males are not territorial in the strict sense, they start to fight as soon as they catch sight of other patrolling male (Kaiser, 1982). Kaiser (1982) further claims; that this behaviour of being aggressive against competitors but not delimiting territories may be an optimal mating strategy for *Cordulegaster* males in their specific ecological situation.

Table 1 *Cordulegaster* species-groups (Pelt, 2006)

Group	Species	Geographic key
boltonii	*princeps*	Moroccan High and Middle Atlas
	trinacriae	SW Italy and Sicily
	picta	Turkey, islands in N and E Aegean sea, SE Balkans
	heros	W and S Balkans
	boltonii	Other parts of Europe or NW Africa
bidentata	*helladica*	S Greece
	insignis	Turkey, islands in N and E Aegean Sea, SE Balkans
	bidentata	Other parts of Europe

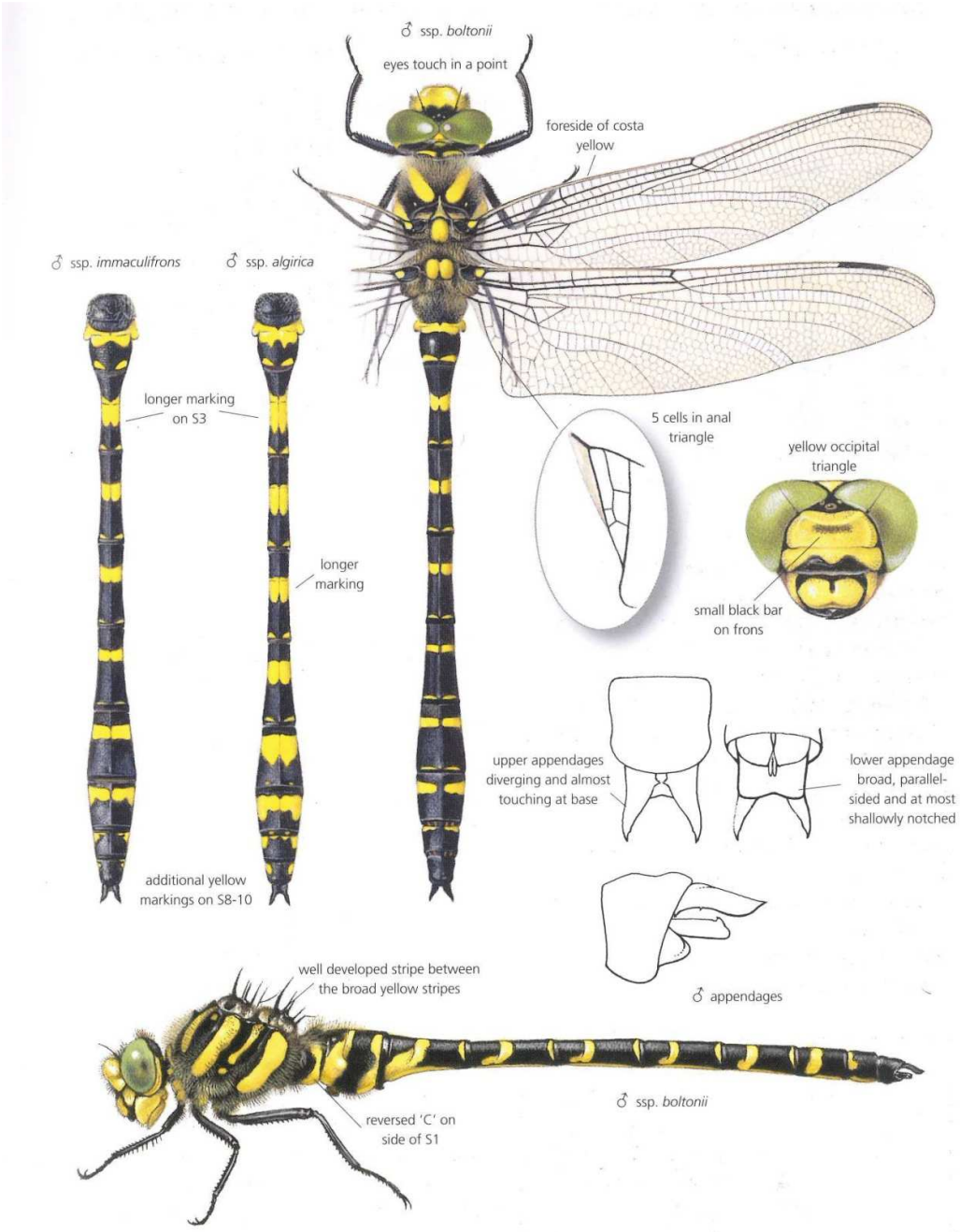


Fig 1 *Cordulegaster boltonii* (Golden-ringed Dragonfly) (Lewington, 2006)

3.2 STUDY SITES

The mark-release-recapture (MRR) survey has been done during two seasons (2010 & 2011) on a relatively dense population of *Cordulegaster boltonii* along three small highland creeks in the Southern Czech Republic. As a study site the Natural

park Česká Kanada was chosen (49.004444° N, 15.180833° E, surface area of 291 km^2, average elevation of 650m), due to its character of relatively unpolluted nature, vast and grown spruce forests (dominated by *Picea abies*) and many sandy bottom creeks. Three of them were chosen according to following criteria: sand-bed, which is prioritized by *Cordulegaster boltonii* larvae and heterogeneous, rather open, full-grown forest with meadows preferred by adult dragonflies and through, accessible terrain along stream banks, so it allows scientist long distance observation and capturing itself. Upper course of Dračice rivulet in a total length of 5900 m, Koštěnický creek (2500 m) and Struha stream (1500 m) qualified according to those criteria. All three locations are separated approximately by 4 km of coniferous forest without any other suitable lotic habitat along the way. Streams were continuously browsed from its spring to its mouth, the point at which they entered a larger body of water (pond, marsh or river). What we considered as an edge point was observed as well as a flight-turning point, an obvious landmark for patrolling *C. boltonii* males.

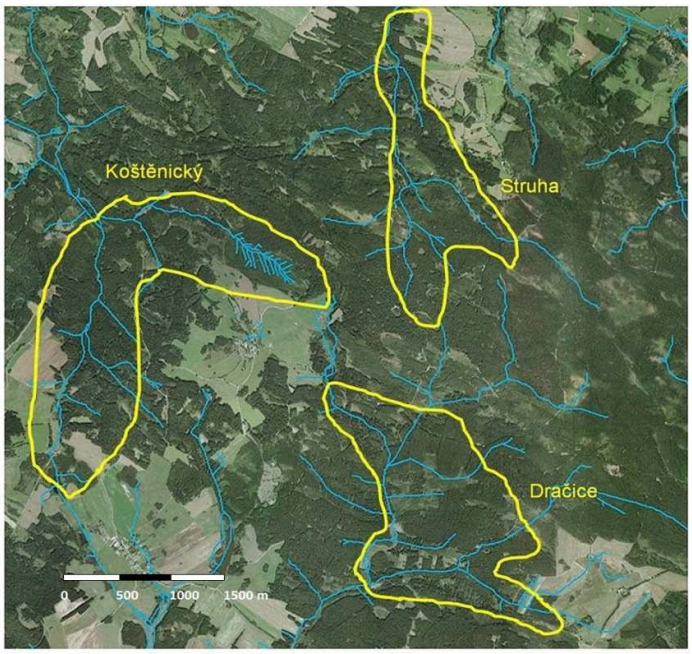


Fig 2 Aerial photo map of study site with highlighted Dračice, Koštěnický and Struha streams

3.3 DATA COLLECTION

Creeks were sampled between 8 July and 16 July 2010 and during three separate week-lasting occasions between 5 July and 5 August 2011, when each week on location was followed by one non-sampling week. Dates were chosen according to main flight period of *C. boltonii*. On each sunny day approximately between 10:00 and 18:00 during the sampling period, group of up to 8 people, divided into couples searched simultaneously all three creeks in a full length of the study area. Considerable effort was made to ensure that sampling effort was constant across creeks. Sexually mature individuals were captured with an aerial net and a unique mark was written on their wings with a permanent marker. They were again released free at the point of capture.

Different marking strategies were used during two seasons. In 2010, a combination of dots or/and crosses, colour specific for each creek, at 10 different prearranged wing positions, was used. This strategy was proved as not exactly convenient especially for later data processing (data transcription into MS Excel and so on). So it was replaced by a unique alphanumeric code consisting of a single letter (D…Dračice, K…Koštěnický, S…Struha), followed by a three digit number. Plus simple pain spot mark allowing identification of flying by individuals recorded on HD camera, installed on stationary spot on the banks of the Koštěnický creek. The location coordinates of each capture as well as subsequent recaptures or sightings were recorded with GPS unit. Field paper protocols containing coordinates and times of each capture/recapture were supplement in 2011 season for data on rear wing length, flight direction (upstream/downstream) and abrasive wear of wings used for age estimate of individuals.

Sampling effort was exclusively focused on male specimens of *C. Boltonii*, since the survey was aimed on local distribution, patrol flight and male territoriality. Females were observed along the streams very rarely, only while mating or oviposition. They spend rest of their adult life foraging in tree canopies, which among others makes them uncatchable and therefore unsuitable for systematic survey.

3.4 DATA ANALYSES

The distances moved were calculated as a sum of Euclidean (straight-line) distances between first and subsequent captures. Gross dispersal distances were calculated for each individual and the maximum and median gross distances were calculated for the studied population and population on each stream separately. "Gross dispersal distance" is being considered as the most ecologically relevant dispersal measure in the context of metapopulation, because it provides an estimate of the total potential distance that an individual can travel. Alternatively the "net dispersal distance" can be calculated, as the distance between locations where individual was first and last captured. However, the ecological relevance of net dispersal distance is unclear given the varying rates of philopatry and uncertainties over what factors affect the tendency to disperse (Beirinckx, Van Gossum, Lejeunesse, & Forbes, 2006) in (Hassall & Thompson, 2012). Because an individual may move back to approximately the same location where it was first captured, this will not tell anything about its ability to disperse. Similarly, individual movements may involve short patrol flights along stream which fulfil different function (e.g. territoriality) than direct dispersal. On the other hand, the potential distance than an individual could move can be calculated as the total sum of these individual flights (Hassall & Thompson, 2012). Next movement pattern estimated was velocity, calculated for each recaptured individual and mean/median velocity for each stream and whole population. Velocity expresses the daily movement rates of animals as it's calculated as distance divided by time ($m.days^{-1}$). For both parameters, gross dispersal distance and velocity, when multiple captures of the same individual on the same day were made, only the first one was included. Euclidean distances were calculated in MS Excel spreadsheet using GPS coordinates.

To see if patrolling males fly independently to each other or whether there is any interaction/coordination among scanning males, as it has been observed during data collecting, fixed spots on Dračice rivulet with most captures (per day), were picked. Times between subsequent captures were calculated, sorted into one-minute-time-interval categories and plotted against their percentage distribution within the sample.

3.4.1 HOME RANGE ESTIMATION

The total home ranges were assed using a linear technique. A linear range span-the distance along the midline of the stream between the maximal upstream and downstream location records was estimated using Ranges8, version 2.13 (Kenward, Walls, South, & Casey, 2008). Software also calculated midline inter-location measures that gave "first to last" measure that represented a sum of all distances recorded (from location to location along the midline) and "location interval" that gave mean value for all distances measured with ± standard error (SE). The length of each with positive value indicated upstream and negative downstream movement. The midline file which was used to define the potential routes between locations needed to be a vector line file. It represented a stream and was created as drawn up line in the middle of a scanned stream image from a map. For each of a pair of locations Ranges found the closest line within the midline file, and calculated the shortest (perpendicular) distance to the line. The distance along the midline between these two points was then added to the two perpendicular distances. This partly eliminated the GPS measurement errors and created more accurate measurement of dragonfly movement, since they in reality did not follow the straight flight lines in between captures but followed the naturally bending stream. For this analyse, only individuals that were captured at least 3 times were included and individuals with long-distance-inter-stream transfers were excluded.

3.4.2 DEMOGRAPHIC ESTIMATES

For testing of presence of the progressive daily values of population size, program Craig for Windows 1.0 (Fric, 2001) was used. Although developed using maximum likelihood theory and based on very simple equations of Craig (1953), there are highly suitable for open/close population structure estimation from MRR data. Despite its simplicity, equations according to Gall (1984) do not overestimate population much.

MRR data were than analysed using a linear model with constraints in the software MARK, version 7.1 (Cooch & White, 2014; White & Burnham, 1999). The Jolly-Seber method for open population estimates was used (Jolly, 1965; Seber, 1973), specifically the POPAN module. POPAN estimates primary parameters: ϕ – residence, which combines the survival probabilities of both marked and unmarked animals between occasions i and $i + 1$; p_i – catchability, the probability of capture of

both unmarked and marked animals that are alive at occasion *i* (combination of mortality and emigration rates); and $PENT_i$ - the probability that an animal would enter the population between occasion *i* and *i + 1*(combines birth and emigration rates). These parameters can be constant (*) or dependent upon time (t). Based from these parameters, several derived parameters can be estimated. For purpose of this survey, simply the total number of individuals (N_{tot}) was estimated (Konvicka, Novak, Benes, Fric, & Bradley, 2008) in (Dolny, Harabis, & Mizicova, 2014). For each sampling stream and year separately, a variety of models was carried out. The most appropriate model was selected based on Akaike's information criterion (AIC) (Akaike, 1973; Anderson & Burnham, 1999). The lower the AIC value, the more suitable the model is for the experimental data. Models with $\Delta AIC \leq 2$ would be considered to be equally supported by field data (Cooch & White, 2014).

3.4.3 DENSITY-DEPENDENT DISPERSION

Effect of high male density on dispersion was tested using software Ranges8, version 2.13 (Kenward, Walls, South, & Casey, 2008). All captures from Dračice rivulet (from season 2011), that had overall highest recapture rate, were plotted into a map, 4 patches with highest male density per 100 m of stream and 3 with low were selected. To assess the density effect, we compared movements of individuals "to", "from" and "within" between these patches using χ-quadrate test (excel add-on algorithms used from http://www.real-statistics.com). For the analysis, we summed up the movement classes over the low and high patches, respectively and we used records only for 2011.

4 RESULTS

4.1 NUMBERS MARKED AND RECAPTURED

In total, 440 males of *Cordulegaster boltonii* were marked in 2010 and 355 in 2011. Of these, 92 individuals were recaptured (20.9 %) at least once in 2010, during 113 recapture events and 100 (28.2 %) males were recaptured at least once, during 171 recapture events in year 2011. The maximum number of times an individual was captured was eight in 2011 and seven in 2010 (Table 3). The longest time between first and last capture was 30 days in 2011, when length of study was 31 days and 8 days in 2010, when study period was exactly 8 days. A breakdown of the numbers marked and recaptured at each stream is provided in Table 2.. It was clear that the Dračice rivulet contained particularly strong population, although the dragonflies were present in reasonable numbers at all creaks. Exception was Struha creek in 2011, when the capture (73 individuals contrary to 114 in 2010, that means 36 % captured animals less) as well as the recapture rate (only 6.8 % in contrast with 20.2 % from 2010) was significantly lower than in previous year. Even though there was not any apparent reason (for example habitat destruction) for a population decline.

Table 2 Total numbers and proportion of male *C.boltonii* marked and recaptured at each stream

			Recapture	
Stream		Marked	Events	%
Dračice	2010	226	45	19,9
	2011	224	138	61,6
Koštěnický	2010	100	45	45,0
	2011	58	28	48,3
Struha	2010	114	23	20,2
	2011	73	5	6,8
Total	2010	440	113	25,7
	2011	355	171	48,2

Table 3 Number of individuals with defined capture history in 2010 and 2011

2010		2011	
individuals	capture history	individuals	capture history
348	1	255	1
77	2	57	2
12	3	27	3
2	4	11	4
1	7	1	5
		2	6
		1	7
		1	8

4.2 MOVEMENT PATTERNS

Nine of the recaptured individuals (7.8 %) transferred between streams in 2010 and one individual (0.6 %) in 2011, giving a total of 10 long-distance movement events. All of them transferred in between streams just once. Longest recorded stream transferring flights was 4821 m (measured as straight line). Shortest period between stream transfers was 3 days, longest 16 days (Table 4). Even though 10 of these inter-stream flights, longer than 3000 m were recorded, most of the population (55 %) was moving within the 250 m range and surprisingly large proportion of individuals (31 %) could be even found within 100 m range, as it is apparent from Fig 3.

Table 4 Long-distance movements between streams

Wing tag	From	To	Distance [m]	Time [days]
D147_10	Dračice	Koštěnický	4541	6
D156_10	Dračice	Koštěnický	4821	8
D175_10	Dračice	Koštěnický	4456	6
D223_10	Dračice	Koštěnický	3249	5
D233_10	Dračice	Struha	3627	3
S176_10	Struha	Koštěnický	3799	3
S282_10	Struha	Koštěnický	3059	3
S285_10	Struha	Koštěnický	3096	3
S287_10	Struha	Koštěnický	3505	3
K035_11	Koštěnický	Dračice	3568	16

The overall median gross dispersal distance recorded in this study was 206 m (geometric mean = 593). The overall median velocity was calculated as 99 m day^{-1} (mean = 268 m day^{-1}) (Table 5). There were 14 individuals whose gross dispersal distance was equal to 0 m, means that they were recaptured on the exact same spot as captured for the first time. One of them was recaptured on same spot after 25 days. Over the course of both seasons 54% of individuals moved less than 250 m.

From 201 individuals captured on fixed point on Dračice rivulet, 35 individuals (17 %) were captured within one minute after previous captured individual (Fig 4).

Table 5 Summary of overall, 2010 and 2011 gross dispersal movements [m] and velocity [m days^{-1}]

	Gross dispersal movement [m]		Velocity [m days-1]	
	Median	Mean	Median	Mean
2010	244	791	347	407
2011	158	415	60	146
Overall	206	593	99	268

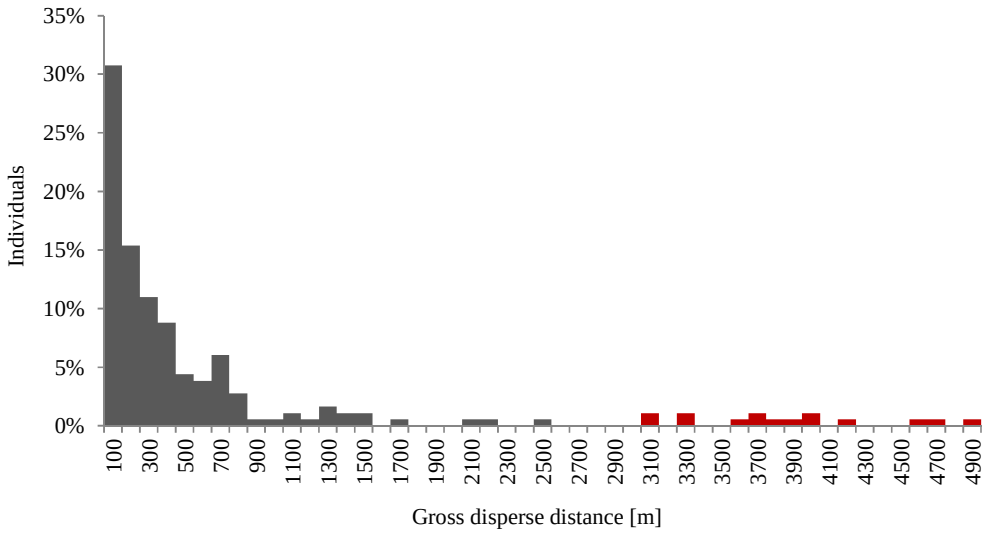


Fig 3 Percentage distribution of "gross disperse distance" in 50-m distance categories. Highlighted with red color are "gross dispersal distances" containing long distance transfers between streams

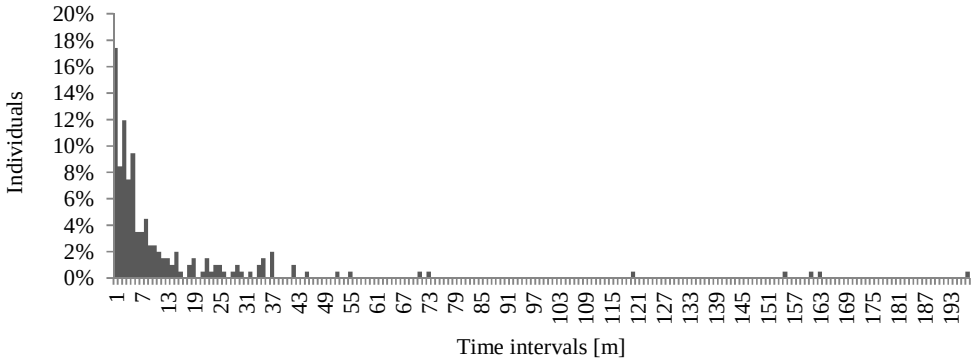


Fig 4 Percentage distribution of time intervals in between subsequent captures on a fixed point on the Dračice rivulet

4.3 FLIGHT DIRECTION

We recorded 198 males flying in direction upstream, 175 individuals were flying downstream and 17 males were sitting on vegetation next to the stream. We can conclude from those records that there was no apparent preference in flight direction (Fig 5).

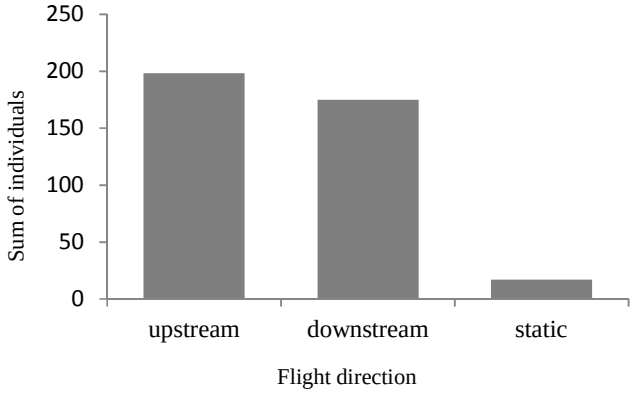


Fig 5 Flight directions of patrolling males *Cordulegaster boltonii*

4.4 HOME RANGE ESTIMATION

Method that most realistically reflect the reality observed, the distance traveled during patrol flight (following the stream), showed similar pattern as calculated gross dispersal distance (straight line). Eleven individuals out of 26 recorded (42 %) had the estimated home range shorter than 250 m on Dračice rivulet and 5 out of 11 individuals were within 250 m home range category on Koštěnický creek. However some males cover larger distances. Six of them were covering part of stream longer than 1000 m (Table 5). Protruding is male D501_11 with estimated long home range of 3549 m. His walkabouts are separately analysed at the end of this part (Table 6).

Table 5 Results of the home range estimation for individuals recaptured more than twice (Ranges8 software). Home range (HR) calculated along the midline as the "linear" home range, which extends to the furthest location, "first to last" is a sum of all distances (from location to location along the midline) and "interval" gives mean value for all distances estimated with ± standard error (SE). The length of each with positive value indicates upstream and negative downstream movement

Dračice					Koštěnický				
	HR [m]					HR [m]			
Wing Tag	linear	first to last	interval	± SE	Wing Tag	linear	first to last	interval	± SE
D591_11	44,5	44,5	22,3	22,3	K065_11	15,5	25,9	8,6	3,5
D593_11	44,5	44,5	22,3	22,3	K059_11	31,9	40,6	8,7	5,1
D594_11	44,5	44,5	22,3	21,8	K064_11	20,3	50,7	16,9	1,9
D077_11	99,6	99,6	49,8	49,8	K000_11	171,0	263,2	89,5	6,6
D105_11	67,2	110,3	27,6	16,7	K238_10	200,3	210,7	70,2	15,7
D127_11	43,1	167,2	55,7	12,6	K236_10	145,2	324,9	162,5	57,3
D110_11	91,7	183,4	36,7	10,5	K235_10	482,1	482,1	241	25,5
D128_11	493,2	188,9	63	32	K182_10	840,0	746,9	180,1	156,1
D202_11	536,3	198,8	66,3	39,1	K030_11	712,6	717,8	239,3	216,3
D033_10	69,1	293,4	103,2	81,6	K032_11	490,5	766,9	383,4	169,8
D104_10	318,1	244,6	122,3	78,2	K158_10	558,6	932,8	155,5	49,6
D104_11	135,2	313,5	78,4	34	median	200,3	324,9	155,5	25,5
D515_11	111,4	474,8	158,8	17,2					
D010_11	311,6	326,6	163,3	26,2					
D137_10	351,1	399,2	199,6	8,2					
D102_11	536,3	476,7	79,5	27,1					
D265_10	106,9	490,7	245,4	193,8					
D588_11	593,4	548,7	274,3	252,3					
D009_11	378,8	682,5	341,2	52,5					
D072_11	378,8	720,3	360,2	33,6					
D017_11	1286,9	1360,5	460	460					
D117_11	1744,6	1744,6	581,5	521,6					
D508_11	1416	2710	903,3	346,8					
D015_11	2809,5	2809,5	1404,8	219,7					
D502_11	2823,9	2860	572	271,7					
D501_11	3548,7	3993,1	570,4	363,8					
median	334,6	362,9	140,55	36,55					

4.4.1 ADVENTURES OF MALE D501_11

Remarkable disperse history was recorded for male D501_11. During 30 days this individual covered cumulative distance of 3993 m, estimated linear home range of 3549 m (Table 6 and map in Fig 6). He was captured for the first time in the most northern area of main stream of Dračice rivulet that was included in this survey. He was monitored there for three days (from 6.7. to 8.7.2011) (Fig 7). During these three days his movement was recorded within approximately 500 m range. Than he was recaptured again after 12 days, on the right tributary stream of Dračice, which enlarged his estimated home range for another almost 500 m. His next recapture happened after 15 more days after last recapture event on the 4.8.2011 and was much more southern. This time he was captured on the left inflow of Dračice. If he moved here by low-above-creek flight (assumed that he did not take shortcut through the forest), he travelled distance of 2703 m. He was captured two more times that same day, within 43 m distance. This suggest that this very same day he probably stayed at this part of Dračice, considering the speed of scanning flight of 1 – 1.5 ms^{-1}, he probably would not be able to travel along whole length of Dračice rivulet to the most northern part, where he was captured for the first time. D501_11 was captured for the last time next day (5.8.2011), 135 m far from previous day capture (Fig 7).

Table 6 Record of movement of a single male D501_11 within 30 days of survey

		Time between captures		
Distance along midline [m]	Date & Time	[hours]	[days]	
	6.7.11 11:09			
115,4	7.7.11 14:57	27:48	1	
510,5	8.7.11 13:47	22:49	1	
485,4	20.7.11 15:41	289:53	12	
2703,4	4.8.11 11:20	355:38	15	
43,1	4.8.11 11:39	0:19	0	
0	4.8.11 14:57	3:18	0	
135,2	5.8.11 11:10	20:13	1	
Total home range 3549 m		Gross time [days]	30	

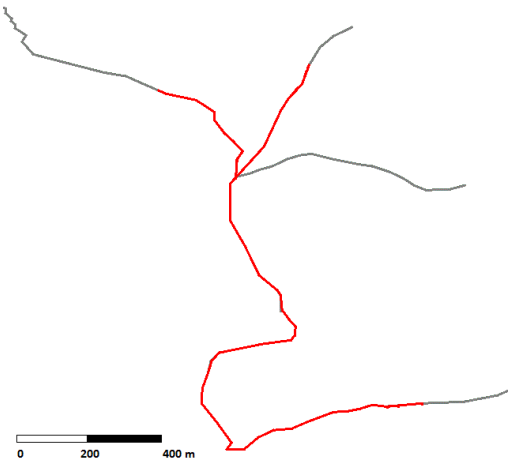


Fig 6 The total home range of male D501_11. Distance of 3993 m covered from 6.7.-5.8.2011 (created in Ranges8), Dračice rivulet

A) B)

Fig 7 The part of stream covered by male D501_11. Between 6.7.-20.7.2011 (A) and than in period 4.-5.8.2011 (created in Ranges8), Dračice rivulet

4.4.2 WANDERING MALES

There were three other males charakterized by wandering pattern similar to male D501_11:

Male D508_11 was first captured on the northenest end of northern right tributary stream of Dračice rivulet. He was recaptured next day not far and than again after 10 days on the junction with main stream of Drčice. After 15 days he returned on a same spot where he was captured for the first two times (Fig7)

First two captures of male D502_11 happened on one of the parts of Dračice with highest male density within one day. He was recaptured twice on a very next day approximately 300 m northern on the junction with northern right tributary stream of Dračice (same place as third capture of D508_11). He was recaptured for a fifth time in a row next day again approximately 300 m northern from the junction. Last recapture was made after 27 days on the most northern end of northern right tributary stream of Dračice rivulet. (Fig. 8).

Last was male D117_11 captured first on the southern left tributary stream of Dračice on one of the places with highest male density. He was still there after two days. Next day he flight downstream of this tributary stream and then upstream of main stream of Dračice, covering the distance of approximately 1200 m. His last capture was next day again back on a spot where he was recaptured first two times (Fig 9)

Table 7 Males with similar wandering history as male D501_11

			Time between captures	
Wing Tag	Capture order	Date & Time	[hod]	[days]
D508_11	1.	6.7.11 13:04		
D508_11	2.	7.7.11 12:59	23:55	1
D508_11	3.	19.7.11 13:25	0:25	12
D508_11	4.	3.8.11 14:47	1:21	15
D502_11	1.	6.7.11 11:19		
D502_11	2.	6.7.11 15:12	3:53	0
D502_11	3.	7.7.11 12:12	20:59	1
D502_11	4.	7.7.11 16:40	4:27	0
D502_11	5.	8.7.11 15:01	22:21	1
D502_11	6.	4.8.11 14:57	23:56	27
D117_11	1.	2.8.11 17:11		
D117_11	2.	4.8.11 15:15	22:04	2
D117_11	3.	5.8.11 9:56	18:41	1
D117_11	4.	5.8.11 11:09	1:13	0

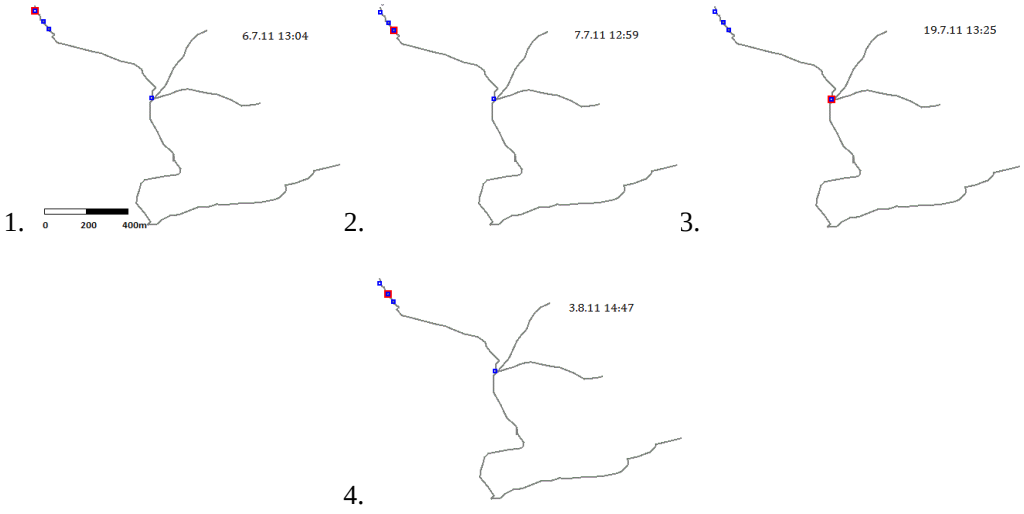


Fig 7 D508_11 – capture history map in chronological order. Created in Ranges8, Dračice rivulet

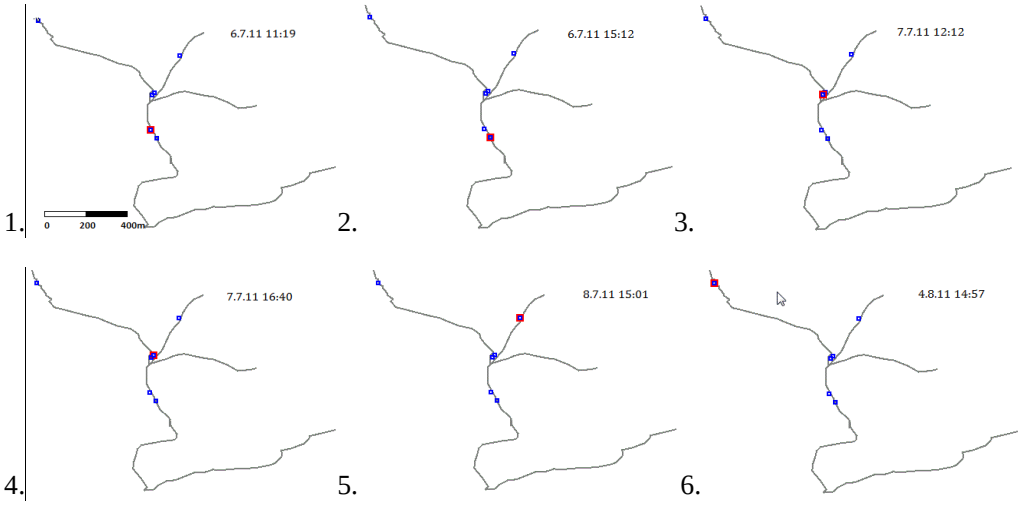
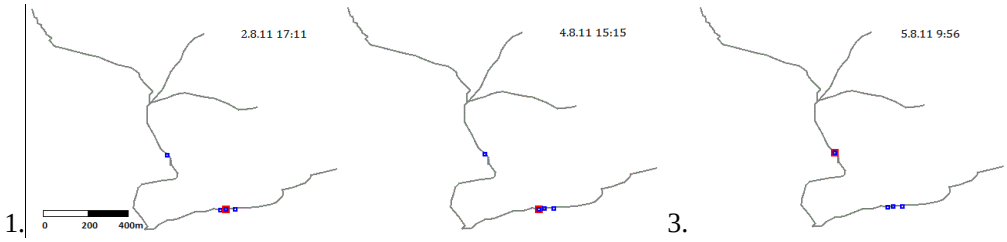


Fig 8 D502_11 – capture history map in chronological order. Created in Ranges8, Dračice rivulet



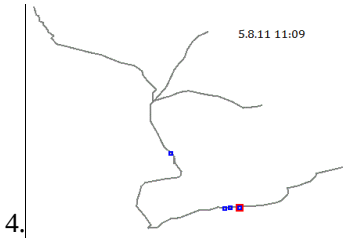


Fig 9 D117_11 – capture history map in chronological order. Created in Ranges8, Dračice rivulet

4.5 DEMOGRAPHIC ESTIMATES

Results from Craig method of population estimates showed decreasing trend in standard error values of estimated population size, for each day (and year) on defined stream separately (Table 7). It can be interpreted as very low immigration rate for all streams. There were some individuals transferring between streams (Table 4), but inter-population flow of individuals is according to those values minor; based on this decreasing trend stream population can be considered rather closed. Very large SE on Struha is caused by low recapture rate on this stream.

Based on lowest value of Akaike's information criterion (AIC), the fully time dependent model $\phi(t)p(t)pent(t)$ was chosen for both sampling years. Total number of individuals (overall population of all three streams together) was estimated from this model as 2163 ± 661 (± SE) *Cordulegaster boltonii* males in year 2010 and 864 ± 131 (± SE) in 2011 (Table 9).

Table 7 Results of the population size estimation from MRR data run in program Craig for Windows 1.0 (Fric, 2001), based on Craig method (1953). Results included ± standard error (SE) of the estimate

Stream		N	± SE	Density [ind./100m]	± SE
Dracice	2010	1330	196	23	3
	2011	590	50	10	1
Kostenicky	2010	315	46	13	2
	2011	175	33	7	1
Struha	2010	673	140	45	9
	2011	1122	498	75	33
Total	2010	2318	382	80	4
	2011	1887	581	92	6

Table 8 Results of the population size (N) estimation, for each stream and year separately. Estimated from MRR data run in program Craig for Windows 1.0 (Fric, 2001), based on Craig method (1953). Results included ± standard error (SE) of the estimate.

2010					2011			
Date	Stream	N	± SE		Date	Stream	N	± SE
8.7	D	1125	786		5.7	D	40000	2000000
9.7	D	196	188		6.7	D	1535	1074
14.7	D	644	367		7.7	D	107	24
15.7	D	486	121		8.7	D	31	7
16.7	D	109	22		19.7	D	179	79
					20.7	D	3	1
7.7	K	30000	1732050		2.8	D	230	159
12.7	K	450	222		3.8	D	64	13
14.7	K	85	28		4.8	D	42	7
15.7	K	51	12		5.8	D	7	1
16.7	K	15	4					
					6.7	K	60000	2449490
9.7	S	20000	1414213		7.7	K	45	22
12.7	S	260	148		8.7	K		
13.7	S	100000	3162277		18.7	K	100	95
15.7	S	223	70		19.7	K	17	7
16.7	S	131	41		20.7	K	0	0
					2.8	K	0	0
					3.8	K	45	22
					4.8	K	2	1
					5.8	K	8	3
					6.7	S	80000	2828427
					7.7	S	399	389
					8.7	S	180000	4242641
					19.7	S	399	389
					20.7	S	15	9

Table 9 Results of the Jolly-Seber analyses, POPAN module in MARK. Primary parameters are ϕ – residence, p_i – catchability and $PENT_i$ - the probability that an animal would enter the population between occasion i and $i + 1$. All parameters are full dependent upon time (t). The most suitable model for given experimental data ($\phi(t)p(t)pent(t)$) was selected based on lowest value of Akaike's information criterion (AIC) and ΔAIC (Akaike, 1973; Anderson & Burnham, 1999). Number of parameters estimated is included (No. Par). Estimated derived parameters is the total number of individuals (N_{tot}) ± standard error (SE)

Stream		AICc	ΔAICc	No. Par	Ntot	± SE	Density [ind/100m]	± SE
Dračice	2010	294.0	0	11	476	82	8	27
	2011	618.3	0	25	542	165	9	55
Koštěnický	2010	197.0	0	9	159	28	6	2
	2011	201.5	0	19	87	15	35	1
Struha	2010	145.7	0	9	238	79	159	10
	2011	93.0	0	10	631	346	421	45
Total	2010	589.9	0	12	2163	661	22	13
	2011	800.1	0	25	864	131	9	3

4.5.1 DENSITY-DEPENDENT DISPERSION

Location of all capture events from Dračice rivulet from year 2011 were plotted in Ranges8 software (Fig 8). Four patches with highest density of captures together with 3 low-density patches were selected. There was 113 individual captures on patch no. 1 (38 ind. / 100 m), from those individual that were captured at least two times: 5 moved "to" patch from outside, 48 were flying "within" the patch and 6 males flown away "from" this certain patch. A bit higher emigration rate was on patch no. 2 (105 individuals in total, 23 / 100 m) were the movement pattern was 5 / 21 / 19 (to / within / from). Patch no. 3 (44 individuals in total, 13 / 100 m) had higher immigration rate, the pattern was 16 / 4 / 6 and last patch, patch no. 4 (42 individuals, 28 / 100 m), shown rather same pattern as patch no. 1 with 7 movements "in", 15 "within" the patch and only 1 male flying away "from" this patch (Table 1).

Table 10 Male densities on 4 selected patches and movements in direction "to", "from" and "within" high and low density patches

	Density		Movement direction		
Patch No.	Total ind.	ind./100m	To	Within	From
1	113	38	5	48	6
2	105	23	5	21	19
3	44	13	16	4	6
4	42	28	7	15	1
sum high			33	88	32
Low density patches					
5	12	3	7	0	4
6	7	2	3	0	1
7	20	5	0	1	6
sum low			10	1	11

The χ-square test confirmed that there is a significant difference ($p = 0.0014$ at $\alpha = 0.05$) in flight patterns between high and low density patches. Apparently, males in high density patches preferred to stay there whereas unfavourable low density patches were readily being abandoned. In more detail, high level of immigration in patch no. 3 and high level of emigration on patch no. 2 is probably given by closeness of those two patches and location of patch 3 on a junction of two tributary streams and main stream of Dračice, resulting in constant flow of individuals. Migration rate in patch no. 7 is probably affected by close patch no. 1 with very high male density (Table 11).

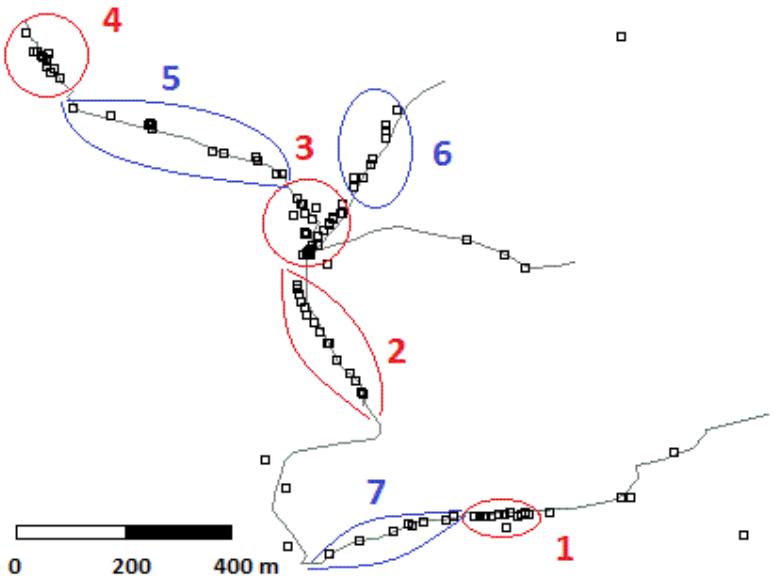


Fig 8 Patches with high male density. Red (no. 1, 2, 3 and 4) are high-density patches, blue are low-density patches (no. 5, 6 and 7). Open squares are plotted captures from year 2011. Created in Ranges8, Dračice rivulet

5 DISCUSSION

The present study showed that adult male population of *Cordulegaster boltonii* has rather restricted local dispersal. We find a high rate of stream fidelity as only few long distance dispersal events between studied streams were detected over course of this two season study. Only ten males (from total amount of 284 recapture events) were recaptured on different stream than the one they were released, resulting in low long-distance dispersal rate of 2.8 %. Such a low dispersal rate is comparable with much smaller species like White-faced Darter *Leucorrhia caudalis* (Charpentier, 1840). It would not be expected this mainly a sedentary libellulid (total length of body 33-37mm and hindwing length 29-32mm), typical percher to have similar dispersal rate of 2,5 % (Keller, 2010) to *C. boltonii*, a flier with greater body mass (total 74-80mm, hindwing 40-47mm) (Dijkstra, 2006). As it has already been proved the body and wing size evolved as a complex trade off between flying ability and energy cost (Marden, 2008) and therefore a larger body size may not necessarily be linked with better dispersal ability (Harabis & Dolny, 2010). *C. boltonii* shows signs of limited dispersal of habitat specialist (Watts, 2004). But we should not forget that this study was done just on adult male specimen of *C. boltonii* and there are differences in tendency to disperse in juvenile (teneral) life stages and between sexes, that we thereby were not able to cover (Corbet 2004). Also rather small geographic ranges of most of species of the *Cordulegasteridae* family can be taken as predicative for their low motivation to dispers over larger spatial scales (Dijkstra, 2006). Observed low level of long distance transfers between streams is reflected in Craig analyse that suggest discreet stream populations being rather closed (Table 8).

Both methods of home range assesment applied on MRR data in order to make assumption about distance covered by patrol fligt showed similar results. If we compare results from gross dispersal movement (straight line distances) and first-to-last range (distance along midline of stream, more accurate mesurement method), that are both sum of all distances recorded for each male, we get approximately half of sampled population covering the distance of 250 m. Median value of gross dispersal distance (GDD) is not comperable with first to last range (FtLR) values, because for GDD estimation we included all recaptures including the individuals that

were recaptured at least once, but for FtLR was necessary to exclude single recaptured individuals and only at least twice recaptured males were included. Linear range (LR) estimation that seemed to be the most ecologicaly relevant, in sence of reflecting the patrol flight, is estimated as an interval in between pair of the most distant locations. Median value of LR estimation give us range of 335 m. But if we exclude from the calculation the longest distance moved by males from bottom of Table 5, for reasons explained later, we are getting closer to estimation of linear range around 250 m. The estimate of velocity as function of distance covered over time (in days), that was effectively used as estimate of dispersal for patchy habitat specialist as *Coenagrion mercuriale* (Hassall & Thompson, 2012) does not seemed to be sensible for a species with life-history as *C. boltonii*. We observed that *C. boltonii* males patrol over a course of a day, in order to calculate the distance they can cover by patrol flight daily we can use our estimate of home range and observed speed of flight 1-1.5 m s^{-1}.

Now let's look closer on a case of male D501_11 and the rest of "wandering" males. The same pattern can be observed in all of them. They were moving within restricted range, we usually captured them three times on a certain location, plus recorded one long transfer flight. Those locations with multiple recaptures could be considered as their home range, since they were observed covering it by patrol flight. And when are those locations compared with map from Figure 10, they significantly matches with patches of highest male density. That single recorded long distance transfer can be interpreted as an attempt to find a new locality. The last one (old one) could have been no longer suitable for too high male density, in other words too demanding intra-specific competition. Low female density could be next reason for leaving former patrolled locality. There could have been as well disturbance of other kind, like predation or inter-specific competition. Capture history of males D508_11 and D117_11 tells the same story: they were patrolling within one of the high-density patches than move to one of the other high-density patches that eventually did not suit them so they moved back on the original location. Male D502_11 changed in two consecutive days two high-density patches, on third day made explorative flight to one of the low density locations, than he was not resighted for almost four weeks to be eventually recaptured for a last time on third high-density location. What we can see behind this behavior? Purpose of patrol flights is to higher chances of

meeting females. For *Cordulegaster* males in their specific ecological situation there is no point in being territorial in usual dragonfly way, as to sit and wait on a potential rendezvous location fighting and chasing away male competitors. Even (in low male density) non-territorial dragonflies tend to shift to aggressive territorial behavior when male density on rendezvous increases (Poethke & Kaiser, 1987). Territorial behavior seems to be advantageous in middle/higher levels male densities, but in highest densities territoriality reaches threshold and breaks down (Pajunen, 1962; Jacobs, 1955). *C. boltonii* males are trying to patrol the stream as extensively as possible to higher their mating chances (Kaiser, 1982). Despite the general expectation *C. boltonii* do not follow ecological rule of "ideal free distribution" and they do not equally spread resources according to their quality. They rather concentrate on best most favourable patches, as the χ-square test of density driven movements showed, leaving the less favourable ones abandoned or scan them rather sporadically. And "less favourable" does not mean deserted, we observed there females as well! Our data suggest that patrolled part of stream in length of approximately 250 m could be sufficient trade-off between chances of female encounter and energy cost.

Unclear is process of decision making that a certain locality is worth of their patrolling. Is it the male density itself that attracts other males to patrol within the same locality? Or do males higher their individual mating chances by recognizing good breeding point on their own, decision based on same features as females, in expectation of more frequent female visits? Based on our field observations (though we did not mark them), female visits were very rare events even in high male density patches. We can estimate their stream visit frequency about 40-50times less than males occurrence. Because of this pronounced female rareness, there doesn't seem to be significant difference in their visits of high and low (male) density patches. Our observation thus suggest that *Cordulegaster* males do not follow "ideal free distribution" concept (Fretwell, 1970) and males are perhaps attracted to patches by occurrence of other males which may result from other reasons then female expectations. The favourable places were usually sun-exposed for considerable part of a day and males use them often for occasional sunbathing.

When it comes to density dependant movement as it is apparent from the Table 11, high male densities challenges males rather to stay and patrol within this probably good breeding site (rendezvous site highly visited by females) than to leave. Those males that left on walkabouts have tendency to come back or they stay patrolling within some other favourable locality. We do not consider those long distance scanning flights to be part of a male home range. We rather categorized them along with inter-stream disperse flights into explorative movements. Question is motivation of males for those long transfer flights between streams. Cost of those flights could be high, in a sense of energy consumption as well as risk of predation or not finding good breeding locality at all. Is the original idea to find new locality to patrol, maybe again locality with either lower competition or higher chances of female encounter. Or is driven by chance, when males find new suitable stream by chance while foraging?

Our observations (male aggregation, home range overlap, no residence in low density patches) make solid evidence against spatial territoriality of males as suggested by Kaiser (1982). Males thus should rise their stakes by other means. In this mating lottery, the high frequency of patrolling flight is on a first place but we do not have sufficient data about daily schedules of individuals. However, there seems to be some non-random interaction, as a significantly large proportion of males were patrolling behind each other within one minute time interval. This behaviour was highly probably not generated by a chance (Table 11). Unfortunately not from data collected nor from observations made we are not able to conclude if there was any kind of cooperation between males patrolling within those short intervals.

Our expectation that there will not be any prevailing trend in flight direction (upstream/downstream) met reality in no significant difference in data collected. Upstream flight preference is known for closely related *Cordulegaster bidentata* (Hykel, 2013; Holusa, 2007). But for *C. bidentata* is given by alternative life-history, when breeding site of *C. bidentata* is restricted to a spring area, and adult dragonflies follow streams to its spring. One directional flight would lower *C. boltonii* mating chances by half, resulting in a not exactly convenient premating strategy.

We are aware of large difference in demographic estimation made by Craig and Jolly-Saber method. Simpler estimation from Craig analyses was considered

being suitable for estimate of imminent population size and closeness of population. More robust design of models made by Jolly-Saber method gave us more reliable population size estimation.

SUMMARY

We carried out mark-release-recapture survey on a *Cordulegaster boltonii* males. Two seasonal study was made on three streams (Dračice, Koštěnický and Struha), with a high male density, in total length of 9900 m, located in natural park Česká Kanada, South Bohemia. We captured and marked 440 individuals and recorded 113 recapture events (26 % recapture rate) in year 2010 and 355 individuals were marked, 171 recapture events made (48 % recapture rate) in 2011. High level of stream fidelity was discovered, reflected in only 10 dispersal events (2.8 % dispersal rate) between streams. Based on length of median dispersal movement and home range estimation we concluded average range of patrolled flight about 250 m in a level of male density observed. Certain pattern was found in male scanning flight, consisting of patrol flight mainly within localities with high male densities and long distance exploratory flight along the course of the stream. Males in high density patches preferred to stay there whereas unfavourable low density patches were readily being abandoned or just rarely scanned. Based on Craig method of demographic estimate we considered stream populations being rather closed, statement that corresponds to low rate of inter-stream migration. Jolly-Saber analyses estimated population size of 1330 ± 196 *C.boltonii* males on Dračice rivulet, 315 ± 46 Koštěnický creek and 673 ± 140 on Struha stream in year 2010 and 590 ± 50 males on Dračice, 175 ± 33 on Koštěnický and 1122 ± 498 on Struha in 2011. There was no preference found in flight direction among patrolling males.

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